STUDIES ON DEEP-SEA PROTOBRANCHIA (BIVALVIA);[1] PROLOGUE AND THE PRISTIGLOMIDAE

H. L. SANDERS[2] AND J. A. ALLEN[3]

ABSTRACT. Great numbers of protobranch bivalves have been found through extensive and continuing sampling of the benthic fauna in the Atlantic at bathyal and abyssal depths. The many new species and varied morphologies that have been revealed indicate that the great radiation of the protobranchs took place in the deep sea. This group is being studied with regard to its comparative anatomy, both soft and hard part; functional morphology *per se* and in relation to abyssal life; changes in form with growth; mode of reproduction; and ecology. An outline classification of major protobranch taxa is given. A new family of the Nuculacea is described, the Pristiglomidae, which contains the genera *Pristigloma* (previously placed in the family Nuculanidae, here raised to superfamily) and *Microgloma*, n.g. Two species of *Pristigloma* are discussed: *P. nitens* and *P. alba*, n. sp. Although broadly distributed, they constitute less than 1% of the total fauna at any one station. They are characterized by extremely reduced gills, exceptionally large palps, and an elongate hindgut. Two new closely related species of *Microgloma*, *M. turnerae* and *M. yongei*, are described. They have a far more circumscribed distribution, both in depth and geography, than *Pristigloma*, *M. turnerae* being confined to the West Europe and Canaries basins and *M. yongei* to the Cape Verde and Angola basins. *Microgloma* are among the smallest bivalves known; miniaturization has been accomplished by reduction in cell size. In the gonads there is a drastic reduction in germ-cell numbers, only two ova maturing at any one time.

PROLOGUE

Since 1961 we have been investigating the deep-sea benthos of the Atlantic from the research vessels CHAIN and ATLANTIS II of the Woods Hole Oceanographic Institution and, to a lesser extent, from the British research vessels SARSIA and DISCOVERY. For the objectives of these studies and the methods used, see Sanders, Hessler and Hampson, 1965; Hessler and Sanders, 1967; Sanders and Hessler, 1969. One facet of our interests concerns the ecology, functional morphology, and evolution of the bivalves. The great array of species and large numbers of specimens allow us to consider for the first time a broad spectrum of morphologies within the Protobranchia from a comparative point of view. Soft-part anatomy and its function as well as shell characters form an integral part of these studies, while growth series are included whenever adequate numbers of specimens are available. All of the studies so far published on the relatively few deep-sea bivalves that were available prior to 1965 have usually considered shell characters and largely ignored the animal within. In fact, in the main, only dead shells have been collected.

The percentage of bivalves present at abyssal depths shows great variance from sample to sample with perhaps a mean of approximately 10 percent by number of the

total benthic abyssal fauna (Hessler and Sanders, 1967). Usually more than 80 percent of these belong to three groups, the Protobranchia, Septibranchia, and Thyasiridae (Allen, 1971). The protobranchs are the dominant group and, in more samples than not, they account for at least 50 percent of the total number of specimens and some 45 percent of the species present. To date we have recorded at least 72 species of the Protobranchia and these encompass most of the known genera and others to be described.

Our task, after sorting the samples into individual species, was that of identification followed by the analysis of hard- and soft-part structures, their function and, in particular, the adaptations to the abyssal environment. Such an investigation is an ongoing process since new samples are continuously being collected. The material from these collections clearly demonstrates the need for a reappraisal of the taxonomic divisions within the Protobranchia. We will, within limits, use the framework of existing classification. Unfortunately, many generic names are known only from shells that have been inadequately described, and figures and existing definitions must be augmented and classified.*

In this and subsequent papers we hope to document the great radiation that has taken place in the deep sea within the subclass Protobranchia. Therefore, it is particularly important that comparative morphology should be adequately described. To begin this task, we will deal first with three extreme groups that require the creation of new family divisions and with the overt objective that they will immediately highlight the problems of identification and rational analysis of this poorly understood bivalve subclass.

To put these studies in a meaningful

framework, it is first necessary to give our interpretations of phylogenetic relationships among the extant major taxa within the subclass Protobranchia. The bases for these interpretations are observations on both hard- and soft-part anatomy of the wide range of morphologies available from our deep-sea collections. No attempt here will be made to review the extensive literature on phylogenies (*i.e.,* Cox, 1959, 1960; Dall, 1895; McAlester, 1964; Purchon, 1958, 1959; Thiele, 1934–1935; Verrill and Bush, 1897; Yonge, 1939, 1959). The primary difficulties are that the different phylogenies proposed are often based on a single morphological system, that only a small subset of the diversity of soft-part anatomies are known, and that morphological features which have been thought to be conservative are not (McAlester, 1964).

Yonge (1939) has shown that within the subclass Protobranchia a greater affinity exists between the Nuculidae and Nuculanidae than between either of these and the Solemyidae. He proposed that two orders be erected, the Nuculoida to include the families Nuculidae and Nuculanidae, and the Solemyoida containing the family Solemyidae. In a recent paper (Allen and Sanders, 1969) we have pointed out that on the basis of shell and soft-part anatomy of *Nucinella serrei* Lamy the enigmatic family Nucinellidae is closest in affinity to the Solemyidae. We now propose that the Nucinellidae be included as a second family within the order Solemyoidea. A diagnosis of the major taxa of the subclass follows:

Subclass **PROTOBRANCHIA**

Bivalves with a foot sagittally and longitudinally grooved with papillate edges; ctenidial filaments flat, platelike, and unreflected.

Order **SOLEMYOIDA**

Protobranch bivalves with a minute triangular palp restricted to an area close to the mouth; ctenidia very large; globular

---

* It is our intention to deposit holotypes in the Museum of Comparative Zoology, Harvard, Massachusetts (MCZ), and when sufficient material is available paratypes will be deposited in the U.S. National Museum and in the British Museum of Natural History.

opisthodetic external ligament often present.

Family SOLEMYIDAE

Shell elongate ovoid and weakly calcified, particularly at the ventral edge; hinge teeth absent; external ligament may or may not be present, dimyarian; extensive ventral mantle fusion; dorsal hood present in stomach; posterior gut diameter very narrow.

Family NUCINELLIDAE

Shell triangulate or nuculid in shape and well calcified; teeth present, composite of series of cardinals and elongate laterals; buttress present on shell around anterior adductor; large external ligament present; monomyarian or extreme heteromyarian, anterior adductor very large; mantle not fused ventrally; dorsal hood absent; posterior gut diameter not markedly narrow.

Order NUCULOIDA

Protobranch bivalves having large palps and palp proboscides, ctenidia not large; external ligament when present never globular.

Hitherto the relationships within the Nuculoida have not been well understood. In contrast to the Nuculidae, which are a sharply circumscribed and well-defined morphological group, the Nuculanidae contain an assemblage of varied morphologies. The problem is further compounded because many of the genera included within the Nuculanidae are known only from their shells. In view of the array of morphological diversity shown by bathyal and abyssal protobranchs, we feel that it is necessary to raise the families Nuculidae and Nuculanidae to superfamily status.

Superfamily NUCULANACEA new superfamily

Type genus: *Nuculana,* Link, 1807

Posterior inhalent current; posterior mantle fusion or development of posterior muscular and/or sensory folds with the formation of posterior siphons, apertures and/or

papillae; mucus glands on mantle, if present, posterior; tentacle present; mouth not at posterior dorsal limit of anterior adductor muscle but at a varying distance from the muscle; ctenidia primarily oriented horizontally; filaments arranged alternately; palps elongate; foot elongate and with narrow neck, papillae moderate in size, heel not sharply separated from the sole; ligament either internal, external, or both; anterior mantle sense organ present; visceral and cerebral ganglia about equal in size.

The tindarid protobranchs represent an anomalous group and, as will be shown, differ in a number of ways from the majority of the Nuculanacea. However, since they agree with the Nuculanacea in many more respects than they do with the Nuculacea, they are tentatively retained within this superfamily.

Superfamily NUCULACEA

Type genus: *Nucula* Lamarck, 1799

Anterior inhalent current; no mantle fusion siphons absent; mucus glands on mantle, if present, anterior; tentacle absent; mouth close to posterior dorsal limit of anterior adductor muscle; ctenidia primarily oriented dorsoventrally or transversely, filaments arranged oppositely; large, broad, deep, almost square palp; foot relatively square and broad-necked, grossly papillate, heel sharply separated from sole; ligament always internal; hypobranchial glands present; anterior sense organ absent; visceral ganglion always smaller than cerebral.

Family PRISTIGLOMIDAE new family

From the review of the protobranchs making up our collections it is apparent that members of the genus *Pristigloma* should be removed from the superfamily Nuculanacea and placed together with a new genus, *Microgloma,* as a second family in a superfamily Nuculacea. They agree with the Nuculacea in all respects. Thus, there is an anterior rather than a posterior inhalent current; lack of mantle fusion; mucus glands of the mantle anterior, not pos-

terior; siphons absent; tentacle absent; mouth at dorsal limit and adjacent to anterior adductor muscle; ctenidia oriented primarily transversely, not horizontally; ctenidial filaments opposite rather than alternate; palp large, broad, deep and almost square rather than elongate; foot relatively square and broad-necked rather than elongate with narrow neck; grossly rather than moderately papillate along margins of the sole of the foot; heel sharply separated from the sole; ligament internal; hypobranchial glands present; visceral ganglion smaller rather than equal in size to the cerebral ganglion.

The two families of Nuculacea can be separated according to the following criteria:

Nuculacid protobranch bivalves that are triangular in shape; ctenidia moderately large with many filaments; cerebral ganglion elongate; hindgut restricted to right side and tightly convoluted .... Family Nuculidae.
Nuculacid protobranch bivalves that are rounded in shape; ctenidia small with reduced number of filaments; cerebral ganglion rounded; hindgut either looped or coiled about both sides of stomach .... Family Pristiglomidae.

We can provide no data as to whether a nacreous layer is present in the pristiglomid shell.

Genus *Pristigloma* Dall, 1900

Glomus Jeffreys, 1876; *non* Gistel, 1848. Dall, 1900; 44. [Type species: *P. nitens* (Jeffreys), original designation.]

Shell fragile, smooth, with at most weak concentric lines; unequal number of teeth on either side of umbo, teeth lamellar or chevron-shaped, anterior teeth few or absent and, when present, confined well medial to level of anterior adductor muscle; umbos raised and posteriorly directed; large internal opisthodetic ligament which is narrow and elongate; hindgut loops rather than coils around stomach; several eggs present in ovary.

Specifically excluded from this genus by the present definition, on the basis of the number, structure, and positioning of the teeth and the shape of the shell, are *Pristigloma* (=*Glomus*) *simplex*, (Smith, 1885) and *Pristigloma* (=*Glomus*) *inaequilateria* (Smith, 1885). The soft parts of these forms are not known.

Pristigloma nitens (Jeffreys, 1876)

Figures 1–6

Glomus nitens Jeffreys, 1876: 433 (Type locality: PORCUPINE Expedition, Station 31; type specimen: U.S. National Museum); 1879: 573, plate XLV, fig. 5. Verrill, 1884: 231; 1885b: 576. Smith, 1885: 248. Dall, 1889: 46. Verrill and Bush, 1897: 53, figs. 1, 2; 1898: 848, plate XCVII, figs. 1, 2.

Pristigloma nitens (Jeffreys). Dall, 1900: 44.

Previous records. Depth range *in* Clarke (1963) = 2933–3477 m. Basins: Labrador, 1 station; North America, 1 station; Argentine, 1 station [Verrill, 1884; Smith, 1885 (as *Glomus*)].

Present records. Depth range = 2022–4853 m: Table I.

Little needs to be amended to the descriptions of shell morphology of this species as given by Jeffreys (1876) and Verrill and Bush (1898). We can add that the narrow, elongate opisthodetic internal ligament extends well posteriorly and is ventrally opposed to and more than half the length of the posterior hinge plate. The anterior plate is very short and thick (Figs. 1, 2).

The soft parts have not been described to date. The mantle edge is not fused, neither is it apposed posteriorly to form exhalent and inhalent apertures. There are three mantle lobes, the inner sensory lobe being moderately produced but nonpapillate. No anterior sense organ and no single posterior mantle tentacle is present. Mantle glands are present lateral and medial to the anterior half of the palps and these extend forward to the mantle edge. Hypobranchial glands are present but these are more circumscribed than in *Nucula* (Atkins, 1936; Yonge, 1939), being restricted to the base of the gill axis and epithelium overlying the ventral surface of posterior adductor muscle. No other specialized gland cells

TABLE I.   RECORDS FOR *Pristigloma nitens* (Jeffreys).

Cruise	No.	Sta.	Depth (m)	Speci-mens	Latitude	Longitude	Gear	Date
				NORTH	AMERICA BASIN			
Chain	58	103	2022	1	39°43.6′N	70°37.4′W	*ES	5.4.66
Atlantis II	30	131	2178	5	39°38.5′N–39°39.0′N	70°36.5′W–70°27.1′W	ES	18.12.66
Chain	50	76	2862	1	39°38.3′N	67°57.8′W	ES	29.6.65
Atlantis II	12	72	2864	6	38°16′N	71°47′W	ES	24.8.64
Atlantis II	24	126	3806	4	39°37.0′N–39°37.5′N	66°47.0′W–66°44.0′W	ES	24.8.66
Chain	50	78	3828	4	38°0.8′N	69°18.7′W	ES	30.6.65
Chain	50	85	3834	4	37°59.2′N	69°26.2′W	ES	5.7.65
Atlantis II	12	70	4680	4	36°23′N	67°58′W	ES	23.8.64
Atlantis II	40	175	4667–4693	2	36°36′N	68°29′W–68°31′W	ES	29.11.67
Chain	50	84	4749	4	36°24.4′N	67°56′W	ES	4.7.65
Atlantis II	24	121	4800	3	35°50.0′N–35°52.0′N	65°11.0′W–64°58.0′W	ES	21.8.66
Atlantis II	24	122	4833	3	35°52.0′N	64°58.0′W	ES	21.8.66
Atlantis II	24	123	4853	2	37°29.0′N	64°14.0′W	ES	22.8.66
				WEST	EUROPE BASIN			
Sarsia		S-50	2379	5	43°46.7′N	3°38′W	ES	18.7.67
				CANARIES	BASIN			
Discovery		6710	2670	2	27°23.6′N	15°39.6′W	ES	19.3.68
Discovery		6711	2988	1	27°14.9′N	15°36.3′W	ES	19.3.68
				BRAZIL	BASIN			
Atlantis II	31	156	3459	2	00°46.0′S–00°46.5′S	29°38.0′W–29°24.0′W	ES	14.2.67
				ANGOLA	BASIN			
Atlantis II	42	194	2864	3	22°54′S	11°55′E	ES	17.5.68
Atlantis II	42	195	3797	9	14°49′S–14°40′S	9°56′E–9°54′E	ES	19.5.68
Atlantis II	42	197	4565–4595	3	10°29′S	9°04′E	ES	21.5.68
Atlantis II	42	196	4612–4360	2	10°29′S	9°04′E	ES	21.5.68
Atlantis II	42	198	4559–4566	5	10°24′S	9°09′E	ES	21.5.68
				ARGENTINE	BASIN			
Atlantis II	60	256	3906–3917	3	37°40.9′S	52°19.3′W	ES	24.3.71

are present except for the typical subepithelial mucus glands concerned with transport of particulate matter within the mantle cavity. The moderately large adductor muscles are relatively ventral in position, more or less oval in shape and clearly divided into "quick and catch" portions. The mouth lies opposite to the inner dorsal edge of the anterior adductor (Fig. 3).

The ctenidia are suspended transversely across the posterior mantle cavity close to the anteroventral border of the posterior adductor muscle. They do not extend anteriorly over the viscero-pedal mass. Relatively few gill plates are present; the number varies with the size of the animal but is usually between 8 and 13. The gill plates lie opposite and do not alternate on each side of the axis of the ctenidium. The inner plates of each axis do not appear to meet
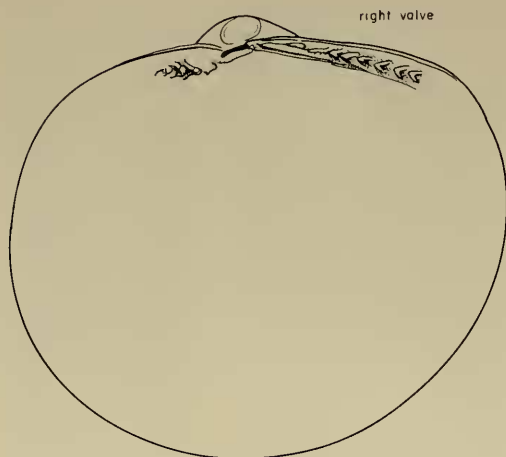
Figure 1. *Pristigloma nitens* (Jeffreys). Internal view of the right valve of a specimen from the original type collection (Specimen 197414, U.S. National Museum, Jeffreys Collection, PORCUPINE Expedition, Station 31, 1381 fathoms).
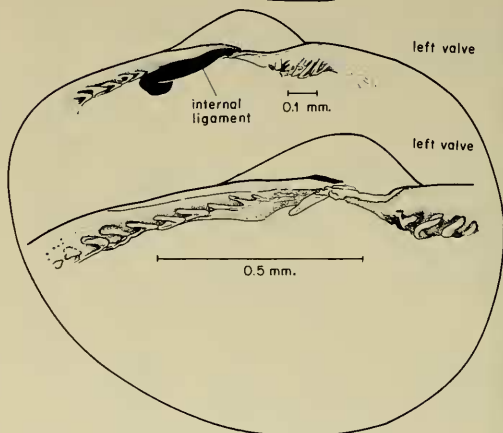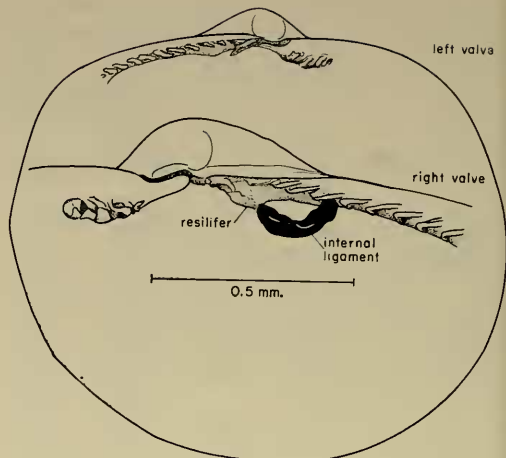

Figure 2. *Pristigloma nitens* (Jeffreys). Internal view of left and right valves of specimens from the Gay Head-Bermuda transect, with enlargements to show detail of hinge structure.

permanently in the midline but hang downwards as very short fingerlike processes. The ctenidial axis is not muscular. It extends posteriorly beyond the first pair of gill plates as a free, tapering projection. Thus the hypobranchial cavity is not entirely separated off from the remainder of the mantle cavity. The paired palps are large and broad and extend from either side of the mouth to the posterior edge of foot; the palp proboscis originates at the posterior dorsal junction of each palp. The contraction of palps and palp proboscides in preserved specimens makes their use in taxonomy questionable. The inner faces of the palps have a large number of folds (22–25) with a morphology essentially similar to that described by Stasek (1961) for *Acila.* The foot is broad with a divided sole; it is moderately large with numerous papillae along the margins. The sole of the foot is ciliated, densely so along central groove and just lateral to it, while the remainder of the sole is sparsely ciliated. A so-called "byssal" gland is present. It is moderately large, ovoid in structure with a central cavity enclosed by glandular secreting cells, and partitioned in a longitudinal,

sagittal plane. Each half opens, side by side, ventral to the heel of foot just posterior to the limit of the divided sole.

The mouth lies close to, but not abutting, the anterior adductor muscle. The oesophagus passes *anteriorly* and dorsal to adductor before turning posteriorly to join a relatively huge stomach lying centrally within the body. The style sac is ventral to the stomach and the hindgut initially extends dorsally and then loops behind the stomach on both sides of the body (Figs. 3, 4a). Four loops are present on each side, *i.e.,* eight sections to each side in a specimen
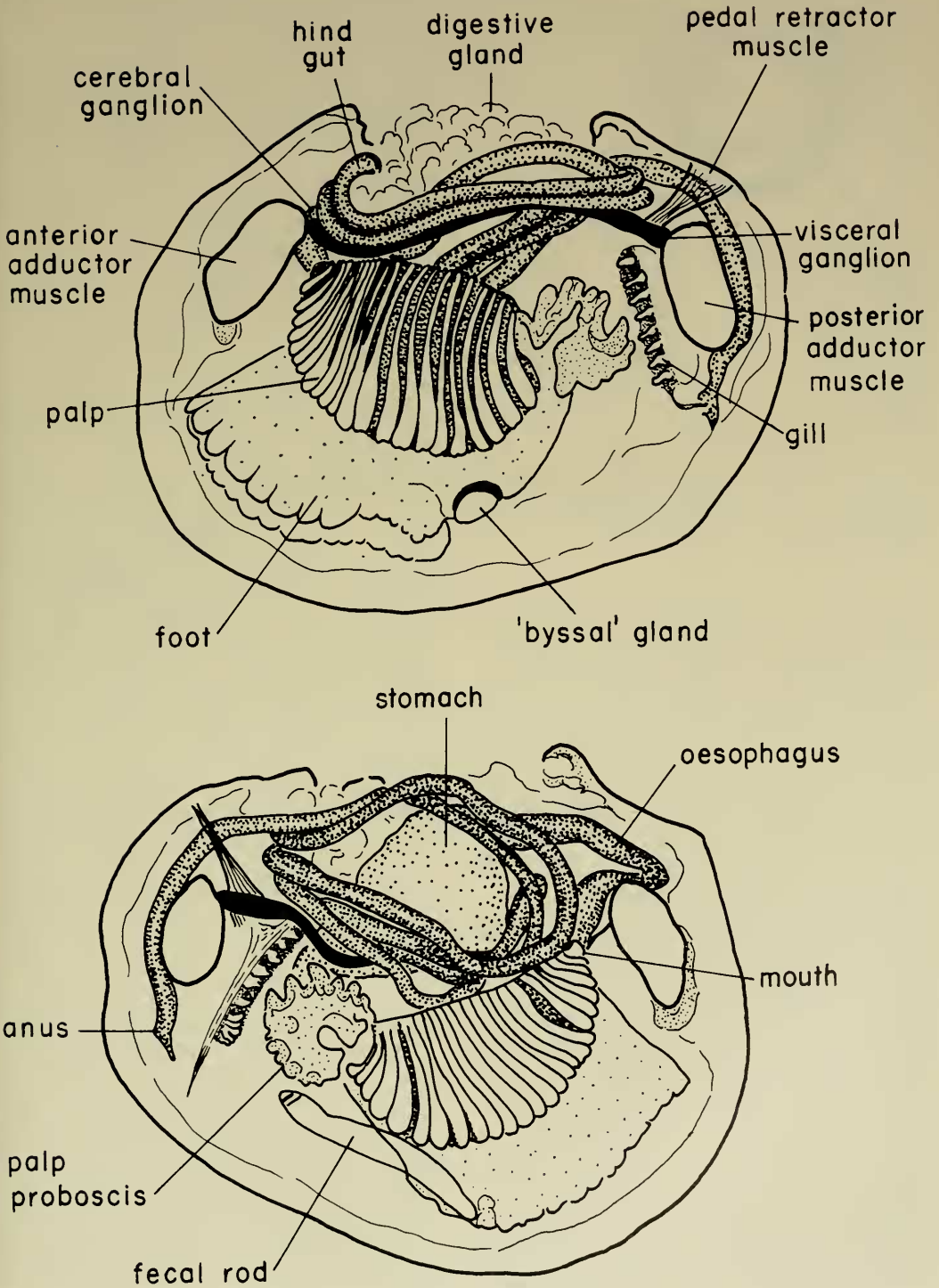
Figure 3.   *Pristigloma nitens* (Jeffreys). Left and right lateral, semidiagrammatic views of the body and mantle organs.
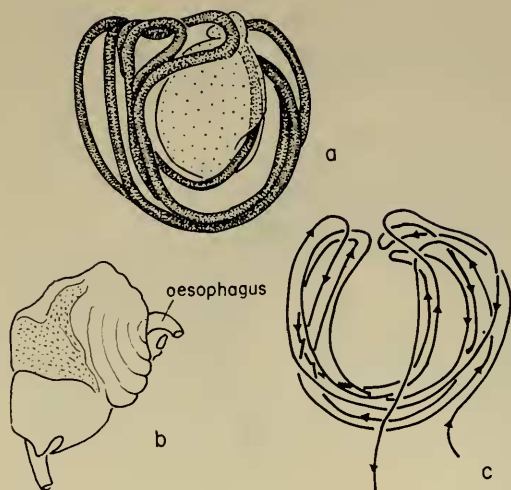
Figure 4. a) Ventral, semidiagrammatic view of the stomach and hindgut of *Pristigloma nitens*; b) lateral view of the stomach of *P. nitens*; c) diagram to show the course of the hindgut of *P. alba*, as seen from the dorsal side of the animal.

transversely sectioned. The terminal loop is on the right side and its distal limb extends posteriorly along the mid-dorsal line over the posterior adductor to the anus, situated above the space between the posterior extensions of the ctenidial axis. The stomach has six sorting ridges and two ducts to digestive diverticula. The visceral ganglia are large and well defined, and, like the cerebral ganglia, rounded. The pedal ganglia are exceptionally large.

Pristigloma nitens shows little proportional change with increasing size (Fig. 5), maintaining a height-to-length ratio of about 0.87 within the length interval of 1.10 mm to 2.72 mm. The maximum length recorded from our samples is 3.54 mm. The prodissoconch in *P. nitens* measures 260 μ in length and the egg size is 190 μ, indicating a direct mode of reproduction (Fig. 6). Nearly 200 eggs at similar stages of development are present in a single specimen, 2 mm, total length. The species is hermaphroditic with concurrently mature eggs and sperm that in the mature animal occupy the greater part of the body space.

Pristigloma alba new species

Figures 4, 7–9

Type locality: ATLANTIS II, Cruise 24, Station 122, in 483 m. Holotype: MCZ 271976. Depth range = 2178–4833 m. We construe *Pristigloma* to be feminine. Records: Table II.

Shell small, fragile, tumid, white, smooth with faintly discernible lines, obliquely rounded in outline but extended anteroventrally; dorsal margin straight; posterior margin short and regularly convex; anterior edge long, with the dorso-anterior margin extended and weakly convex and the ventro-anterior margin short and strongly convex; ventral edge gradually sloping ventroanteriorly; umbos proportionately large and swollen with beaks directed slightly posteriorly; no lunule, escutcheon, or external ligament present; opposing edges of valves raised both posterior and anterior to the umbo and forming a crest. Hinge plate weak, narrow, straight, and separated by a small notch in the equally lengthened anterior and posterior parts. Teeth few, lamelliform in shape, horizontally directed, parallel and overlapping; posterior row of three teeth with the proximal member half the length of the others; anterior hinge plate devoid of teeth but with a faint furrow in the right valve and two in the left. Large internal, elongate opisthodetic ligament extends obliquely posterior as a narrow, elongate, concave resilifer immediately below the hinge to the level of the distal edge of the proximal tooth. Neither muscle scars nor pallial line evident (Fig. 7a, 7b).

Mantle similar to *P. nitens* with no fusion or adhesion to form exhalent and inhalent apertures. Adductor muscles equal, the anterior extending below the level of the mouth. Hypobranchial gland cells present in the region of the gill axis and dorsally overlying the floor of kidney anterior to the posterior adductor muscle. The position of the palps and ctenidia is similar to *P. nitens* but their relative proportions differ greatly. Ctenidia considerably reduced, being restricted to two pairs of oppositely placed

Figure 5. Lateral views of a series of specimens of *Pristigloma nitens* to show changes in shape with increasing size. Features of the soft-part anatomy, seen through the shell, are indicated.

plates. Palps very large (with approximately 17 ridges) and take up much of the lateral area of the mantle, and cover most of the lateral surface of the body/foot; palp proboscides, in a contracted state, short and thickened. Foot large, differing from *P. nitens* in that the sole is very broad and the fringing papillae are relatively large and few in number (Fig. 8), consisting of 5–6 broad laterals, 4–5 smaller posterolaterals on each side and 5 smaller frontal papillae; heel very large, hooked ventrally, and widely separate from foot; "byssal" gland large, from which an elongate groove extends and terminates at the center of the sole of foot.

The configuration of the gut is similar to that of *P. nitens*, except that there are five pairs of hindgut loops closely applied to each other* (Fig. 4c). Oesophagus lacks an anterior loop above adductor muscle and the anus does not extend as far into hypobranchial space as it does in *P. nitens* (Fig. 8). Stomach relatively large yet simple with but two sorting ridges. Ganglia

---

* It is difficult to determine both from sections and from whole mounts whether some parts of the hind gut encircle the stomach rather than form loops as in *P. nitens*. Nevertheless, as far as can be seen there are no encircling sections, but the loops to the right and left of the body overlap in front of the stomach.

TABLE II. RECORDS FOR *Pristigloma alba* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Speci-mens	Latitude	Longitude	Gear	Date
				NORTH AMERICA BASIN				
Atlantis II	30	131	2178	2	39°38.5′N–39°39.0′N	70°36.5′W–70°37.1′W	ES	18.12.66
Atlantis II	12	72	2864	2	38°16′N	71°47′W	ES	24.8.64
Atlantis II	12	64	2891	1	38°46′N	70°06′W	ES	21.8.64
Atlantis II	24	126	3806	2	39°37.0′N–39°37.5′N	66°47.0′W–66°44.0′W	ES	24.8.66
Chain	50	85	3824	4	37°59′N	69°26.2′W	ES	5.7.64
Atlantis II	40	175	4667–4693	6	36°36′N	68°29′W–68°31′W	ES	29.11.67
Chain	58	100	4743–4892	2	33°56.8′N	65°47′W	ES	1.5.66
Atlantis II	24	121	4800	3	35°50.0′N–37°24.0′N	65°11.0′W–65°54.0′W	ES	21.8.66
Atlantis II	24	125	4825	1	37°26.0′N–35°50.0′N	65°50.0′W–64°57.5′W	ES	23.8.66
Atlantis II	24	122	4833	10	35°52.0′N	64°58.0′W	ES	21.8.66
				CANARIES BASIN				
Discovery		6709	2351	2	27°29.8′N	15°20.1′W	ES	18.3.68
Discovery		6711	2988	1	27°14.9′N	15°36.3′W	ES	19.3.68
				BRAZIL BASIN				
Atlantis II	31	156	3459	2	00°46.0′S–00°46.5′S	29°28.0′W–29°24.0′W	ES	14.2.67
				ANGOLA BASIN				
Atlantis II	42	195	3739	8	14°49′S–14°40′S	9°56′E–9°54′E	ES	19.5.68
Atlantis II	42	197	4592–4597	1	10°29′S	9°04′E	ES	21.5.68
Atlantis II	42	198	4559–4566	7	10°24′S	9°09′E	ES	21.5.68
				ARGENTINE BASIN				
Atlantis II	60	242	4382–4405	2	38°16.9′S	51°56.1′W	ES	13.3.71

(including visceral) are well defined and rounded.

The species is hermaphroditic with concurrently mature eggs and sperm; about 20 mature eggs, 115 μ in diameter,[**] were present in a specimen 1.2 mm total length with a prodissoconch 190–200 μ in length. Egg and prodissoconch lengths suggest that *P. alba* has a lecithotrophic mode of reproduction (Ockelmann, 1965).

There is no obvious change in size di-

mensions with growth within the range of lengths available, 0.45 to 1.90 mm, although the larger specimens may be proportionately less elongate (Fig. 9). The approximate length:height:breadth ratio is 1.00: 0.79:0.63.

This minute clam can be separated from all other known species of nuculoid protobranch bivalves by its inflated shape, large umbos, very fragile shell, absence of teeth on the anterior hinge plate, lamellar form and horizontal positioning of the posterior teeth, and by the broad foot with few large papillae, and the closely packed hindgut loops.
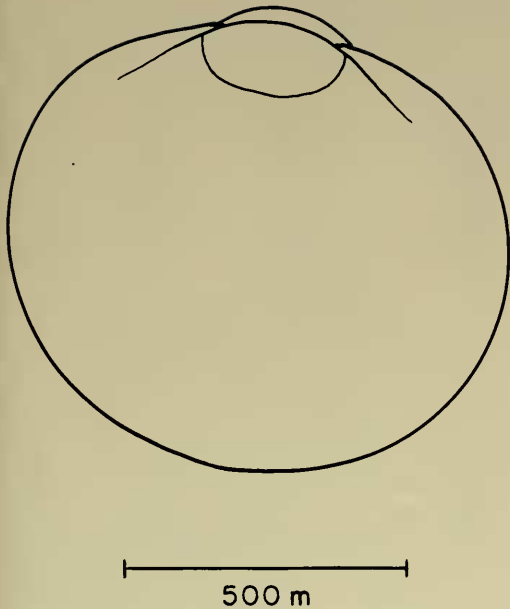
[**] The eggs are considered mature in that they occupy the total available space, there being a very large quantity of yolk present together with a mature nucleus and large, heavily staining nucleolus.

Minute; strong, robust shell with concentric ridging; equal number of teeth on either side of the umbo; teeth taxodont and extend along the hinge to the level of the posterior edge of the adductor muscles; umbos low in profile and medially directed; internal ligament amphidetic and bean-shaped; hindgut coils rather than loops about stomach; at most two mature eggs present in ovary.

This genus differs from *Pristigloma*, in that the hinge is symmetrical on either side of the umbo, having a robust shell, chevron-shaped teeth only and an internal amphidetic ligament. The soft anatomy differs in having the hindgut coiling rather than looping about the stomach.

Only two species are known of this genus and these are restricted to the eastern Atlantic.

Figure 6. Lateral view of a young specimen of *Pristigloma nitens* with a well-defined prodissoconch.

Genus *Microgloma* new genus

Type species: *Microgloma yongei* (new species). We construe *Microgloma* to be feminine.

Microgloma yongei new species

Figures 10–14, 21

Type locality: ATLANTIS II, Cruise 42, Station 200, in 2644–2754 m. Holotype: MCZ 271971. Depth range = 1964–2031 to 2754 m. **Records:** Table III.
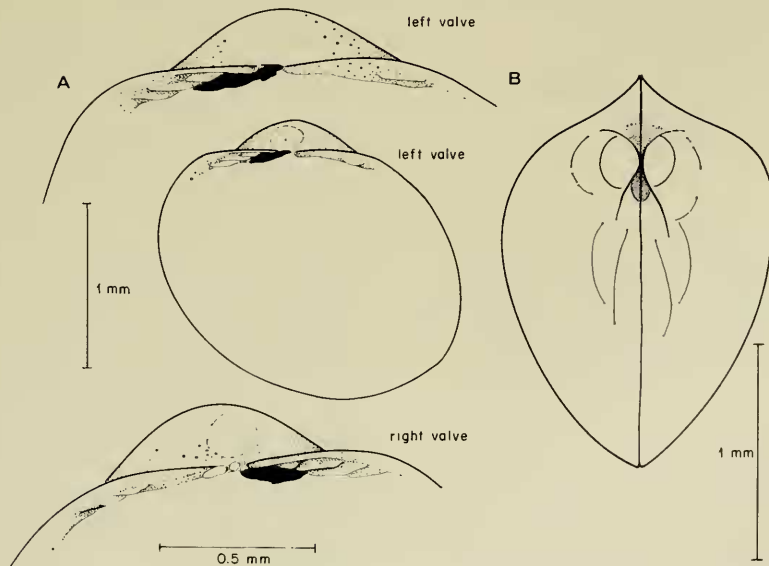

Figure 7. *Pristigloma alba* (Sanders and Allen). a) Lateral internal view of left valve and enlarged hinge detail of right and left valves; b) dorsal view of shell.

TABLE III.   RECORDS FOR *Microgloma yongei* NEW SPECIES.

Cruise	No.	Sta.	Depth (m)	Speci-mens	Latitude	Longitude	Gear	Date
			CAPE VERDE BASIN					
Atlantis II	31	145	2185	19	10°36.0′N	17°49.0′W	ES	6.2.67
			ANGOLA BASIN					
Atlantis II	42	200	2644–2754	90	9°41′S–9°43.5′S	10°55′E–10°57′E	ES	22.5.68
Atlantis II	42	201	1964–2031	18	9°29′S–9°25′	11°34′E–11°35′	ES	23.5.68
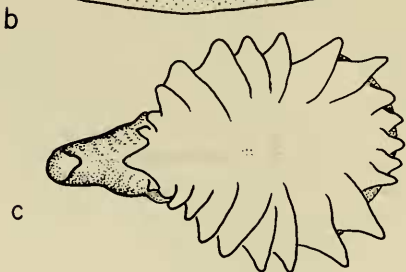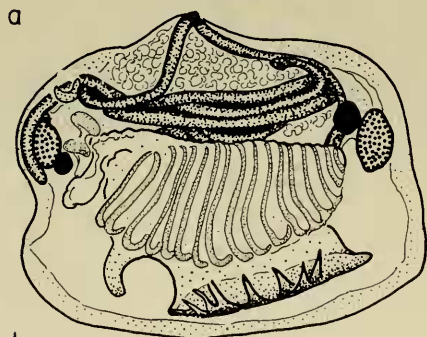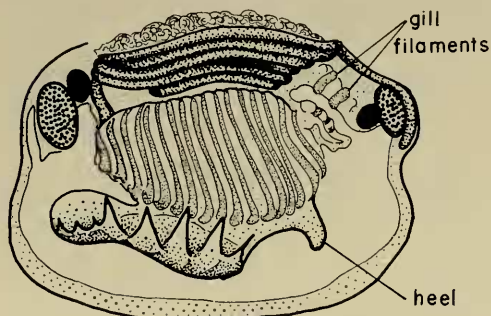
Figure 8. a) Left and b) right lateral, semidiagrammatic view of the body and mantle organs, and c) ventral view of the papillate foot, of *Pristigloma alba.*

Shell minute, robust, with strong concentric ridges at the margins that gradually become less obvious towards umbonal re-gion; elongate oval in outline and extended anteriorly; dorsal margin slightly curved; posterior margin short and smoothly but strongly rounded; anterior margin long with both dorso- and ventro-anterior margins weakly convex and evenly rounded; umbos small, very low in profile, posterior in position, and medially directed; no escutcheon or lunule. Hinge plate with a narrow, elongate, amphidetic internal ligament; posterior hinge plate slightly shorter and straighter than the anterior; three or four chevron-shaped teeth present in the anterior and posterior tooth series (Fig. 10).

Neither inhalent or exhalent apertures present nor an anterior mantle sense organ. Adductor muscles equal in size. Few hypobranchial gland cells present in the epithelia of the ctenidial axes. No specialized mantle glands present. Gills set transversely across the posterior part of the mantle cavity, anterior to the posterior adductor; six pairs of fingerlike gill plates, each pair oppositely attached to axis; posterior axial extension present as in *Pristigloma.* Palps large, not rectangular, but somewhat fan-shaped, each with 12 internal ridges, and extend to the posterior edge of foot. Mouth set slightly behind the anterior adductor muscle. Stomach moderately large with 3 sorting ridges and 2 ducts to the digestive glands; style sac moderately large with a combined midgut from which the hindgut passes dorsally. Subsequently the hindgut is arranged so that there is 1 loop on left side of body, 3 coils encircling the stomach and 1 loop on right side of body in that sequence. The final arm of the last loop is me-
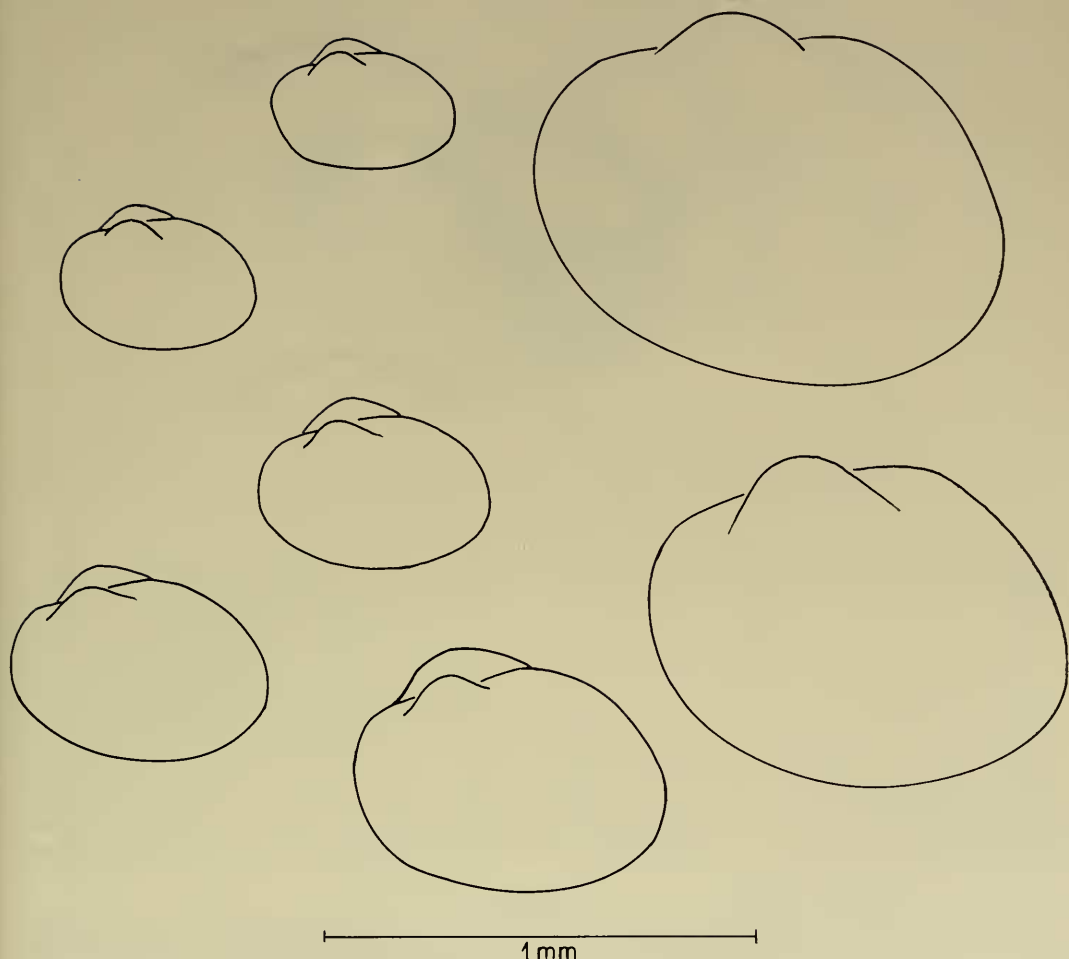
Figure 9. *Pristigloma alba* (Sanders and Allen). Lateral views of a series of specimens to show changes in shape with increasing size.

dian dorsal in position and leads to the anus. Anteriorly, the coils of the hindgut pass from left to right in front of oesophagus thus displacing it posteriorly. Foot broad with 12–14 fringing papillae to the right and left margins of the sole; heel very prominent, pointed and distinct from the sole; a moderately developed "byssal" gland internal to where foot and heel join. Nervous system similar to that in *Pristigloma* except that the visceral ganglia are as large and as well defined as the cerebral (Figs. 11, 12).

Hermaphroditic with but 2 concurrently mature eggs, one very slightly in advance of the other in its development; sperm relatively few in number, forming cap to the outside of the ova (Figs. 13, 19). Prodissoconch length of 290 μ (Fig. 10c); size of mature egg 120 μ.

M. yongei shows no obvious proportional changes with growth (Fig. 14), having a height-to-length ratio of about 0.76 and a breadth-to-length ratio of 0.55, reaching a maximum length of 1.1 mm. The absolute size range in our sample was 0.76 to 1.11
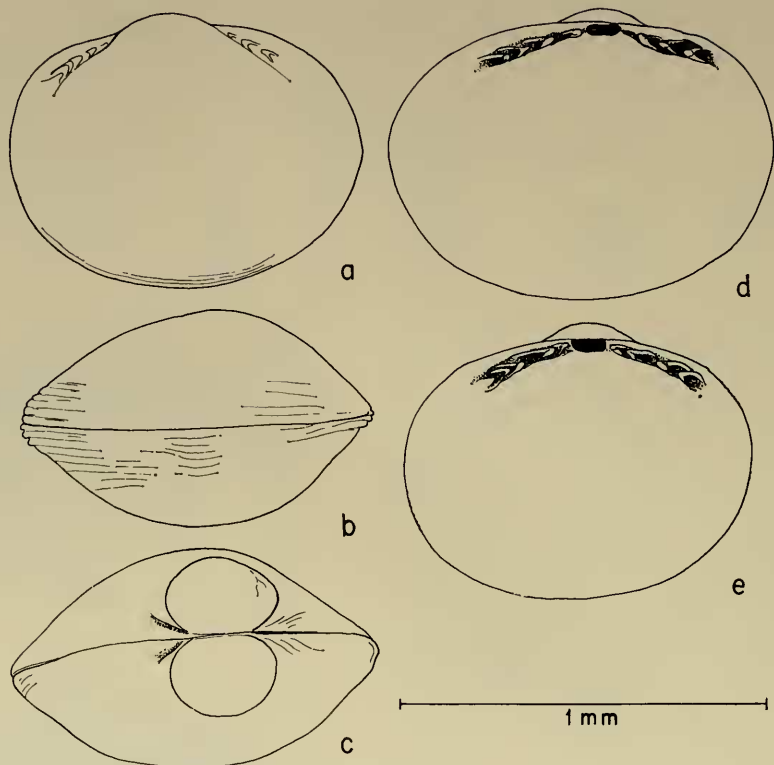
Figure 10. *Microgloma yongei* (Sanders and Allen). Shell characters, a) lateral view of right side; b) ventral and c) dorsal view of shell, showing the prodissoconch; d and e) internal views of the left valves showing individual variation in form.

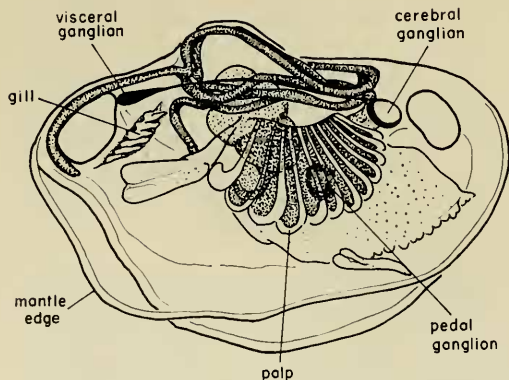mm; the shape of the histogram (Fig. 21) indicates that the larger sizes were adequately sampled but that increasing proportions of the smaller sizes were lost through the meshes of the net.

The species is named in honor of Sir Maurice Yonge, a leading scholar and outstanding mentor in Malacology.

Microgloma yongei can be separated from the closely related *M. turnerae* by its proportionately greater length, the less oblique descent of the dorso-anterior margin, the lower profile of the umbo, the smaller internal ligament, the narrow hinge plate, and the larger prodissoconch.

Figure 11.   Right lateral, semidiagrammatic view of the body and mantle organs of *Microgloma yongei.*

Microgloma turnerae new species

Figures 15–21

Type locality: SARSIA Cruise, Station S-65, in 1922 m. Holotype: MCZ 271972. Depth range = 952–2351 m. Records: Table IV.
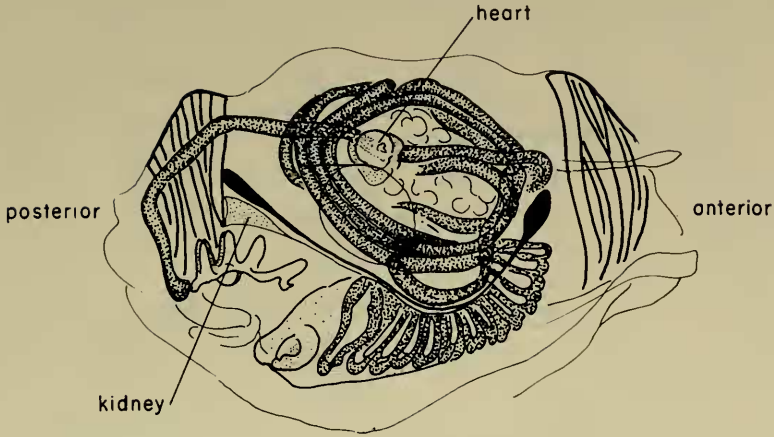
Figure 12.   Dorsal, semidiagrammatic view of the body and mantle organs of *Microgloma yongei.*

Shell minute, robust, with strong concentric lines particularly along the shell margin and with faint radiating striae; subovate in outline and extended anteriorly; dorsal margin straight; posterior margin short and smoothly rounded; anterior edge long, with the dorso-anterior margin weakly convex and slightly longer than the more convex ventro-anterior edge; ventral margin weakly though evenly convex; umbos not prominent, low in profile, posterior in position and medially directed; neither lunule nor escutcheon present. Hinge plate moderately strong with a large, bean-shaped amphidetic internal ligament; posterior hinge plate shorter and straighter than the slightly ventrally sloping anterior hinge plate. Three moderately strong chevron-shaped
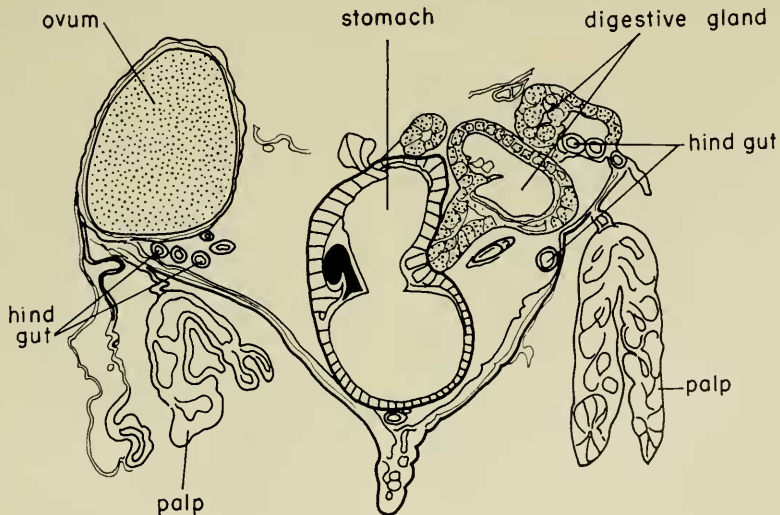

Figure 13.   *Microgloma yongei* (Sanders and Allen). Transverse section through stomach, digestive gland, hindgut, ovum, and palp.

TABLE IV.   RECORDS FOR *Microgloma turnerae* NEW SPECIES.

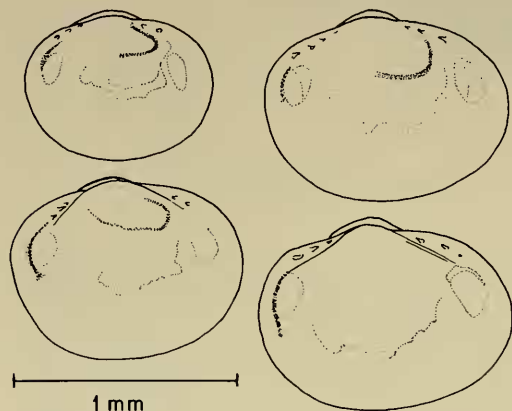| Cruise	Sta. No.	Depth (m)	Speci-mens	Latitude	Longitude	Gear	Date
			WEST EUROPE BASIN				
Sarsia	S-61	952	2	46°20.5′N	4°36′W	ES	19.7.67
Sarsia	S-44	1739	11	43°40.8′N	3°35.2′W	ES	16.7.67
Sarsia	S-65	1922	148	46°15′N	4°50′W	ES	25.7.67
			CANARIES BASIN				
Discovery	6709	2351	5	27°29.8′N	15°20.1′W	ES	18.3.68

Figure 14. Lateral views of a series of specimens of *Microgloma yongei* to show changes in shape with growth.

teeth and a distal incipient protuberance on both the anterior and the posterior hinge plate (Fig. 15).

The soft parts are similar to those of *M. yongei*. The mantle characters differ only in that the adductor muscles are appreciably larger (average muscle scar/lateral mantle area ratio in *M. turnerae* 0.44/1, and in *M. yongei* 0.52/1). The palps are somewhat smaller than those of *M. yongei*, each with 13–14 ridges. The basic plan of the hindgut is similar in the two species except that all the coils are adjacent and ventral to the digestive gland in *M. turnerae*, whereas in *M. yongei* part of one coil lies dorsal to the digestive gland on the right side and alongside the final section of gut leading to anus (Figs. 11, 16, 17, 18, 19).

Microgloma turnerae shows little proportional change with growth (Fig. 20), maintaining a height-to-length ratio of about 0.80 and a breadth-to-length ratio of 0.54. It reaches a maximum length only slightly greater than 1 mm, and we believe that this may be the smallest known free-living bivalve. Its absolute size range in our samples is from 0.72 to 1.03 mm. The shape of the histogram in Figure 21, with a precipitous drop in numbers at lengths greater than 0.98 mm and a rapid though more gradual decline in numbers at lengths less than 0.94 mm, suggest that the larger sizes were adequately sampled but the progressively smaller sizes were lost through the meshes of the net (0.5 mm openings at the cod end) in ever-increasing proportions.

M. turnerae is hermaphroditic with two concurrently maturing eggs. The sperm are relatively few in number and cup the outside of the ova. A prodissoconch length of 260 μ (Figs. 15c, 18, 19) would indicate direct development (Ockelmann, 1965), yet the egg size of 120 μ falls within the size range of lecithotrophic development. Possibly the remarkably small size of both species of *Microgloma* imposes a severe limitation on the egg diameter that can pass through the oviduct, yet, with an egg number of two, development is likely to be direct if the species is to survive. Such an interpretation is consistent with the finding that the prodissoconch length is disproportionately large when compared with actual egg size.

This species is named in honor of Dr. Ruth Turner of the Museum of Comparative Zoology, Harvard University, a dedicated and enthusiastic scientist and re-
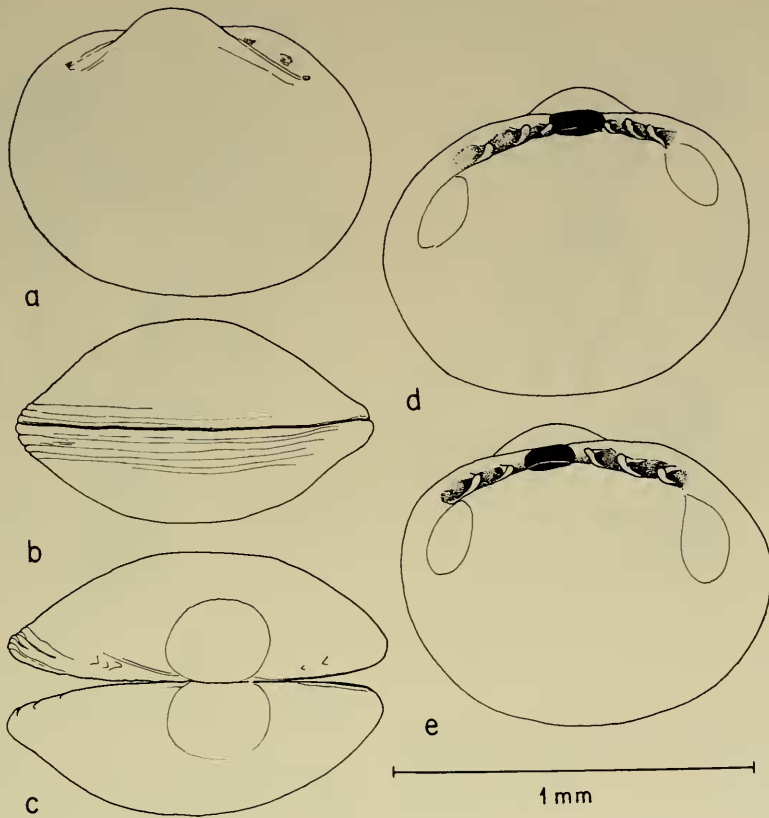
Figure 15. *Microgloma turnerae* (Sanders and Allen). Shell characters, a) outer lateral view of right valve, b) ventral view and c) dorsal view of shell, showing the prodissoconch; internal view of d) right and e) left valves.
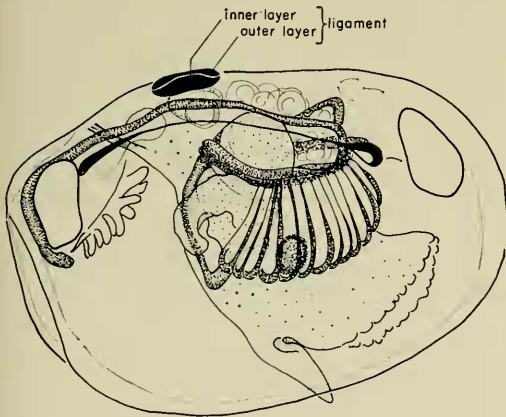

Figure 16. Right, lateral, semidiagrammatic view of body and mantle organs of *Microgloma turnerae*.

spected colleague, for her significant contributions to malacology.

FUNCTIONAL MORPHOLOGY OF THE SOFT-PART ANATOMY IN THE PRISTIGLOMIDAE

No organ system evolves in isolation; it can only be understood in relation to its interaction with other systems and structural units. Animal form and function are the resultants of such interdependent relationships in response to environmental stimuli. Thus, in the case of the family Pristiglomidae, the rounded form can be correlated, in part, with the absence of mantle fusion or modification. Since neither siphons nor tentacles are present, there is
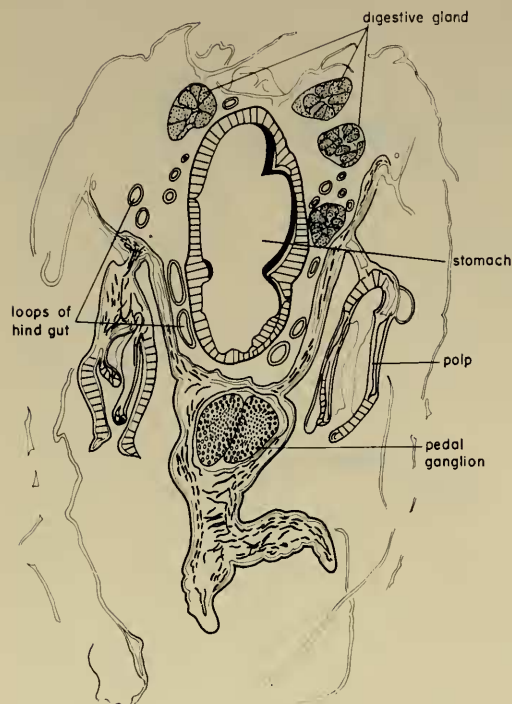
Figure 17. *Microgloma turneroe* (Sanders and Allen). Transverse section through stomach, digestive gland and pedal ganglion.
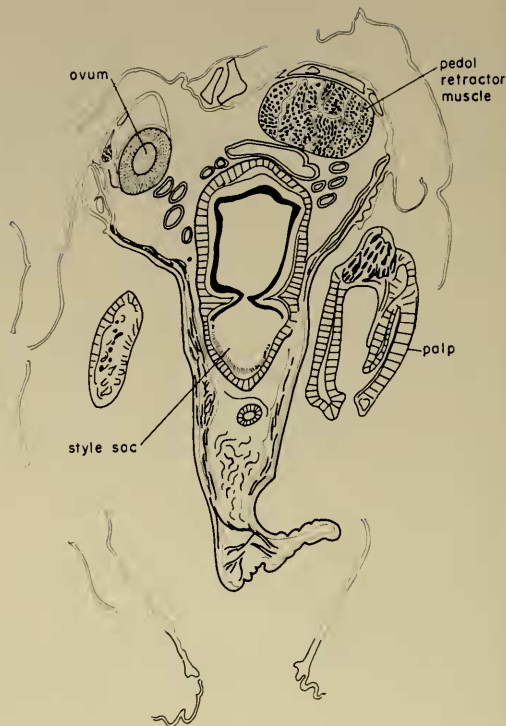
Figure 18. *Microgloma turneroe* (Sanders and Allen). Transverse section through stomach and second ovum.

no morphological reason for the shell to be rostrate and posteriorly elongate. Because the inhalent current must be anterior and ventral and the exhalent current posterior, a direct one-way flow system results.

Flow patterns within the mantle cavity of those species with an anterior and ventral incurrent, such as *Pristigloma* and *Microgloma*, seem to be related both to the ventral positioning of the anterior adductor muscle and the position of the mouth close to the posterior dorsal edge of that muscle (Allen, 1958, 1968). The adductor may act as a baffle or wall, which regulates the direction of flow of the adjacent currents away from the region of the mouth and broadly directs the flow of water away from the anterior and towards the posterior part of the palps, thus ensuring that maximum sorting takes place at the palp surfaces.

The position of the ctenidial axis is also related to the position of the inhalent current area. In the Nuculanacea the inhalent current is posterior and concentrated in a narrow intake diameter and flows immediately along and directionally parallel to the length of the ctenidia, whereas in the Nuculacea, and in *Pristigloma* and *Microgloma* in particular, the incurrent flow is broad, less directional, and not adjacent to the ctenidia. The position of the ctenidia in the Nuculacea are distant from the point of entry and set at right angles to the flow (Fig. 22).

It was shown earlier (Allen and Sanders, 1966) that, in the tellinacean *Abra*, there is an inverse relationship between size of palp and size of ctenidium, and that when the species of *Abra* are arranged in increasing depth range, there is a progressive reduction in ctenidium size. In general, this relationship also holds for the Nuculacea.
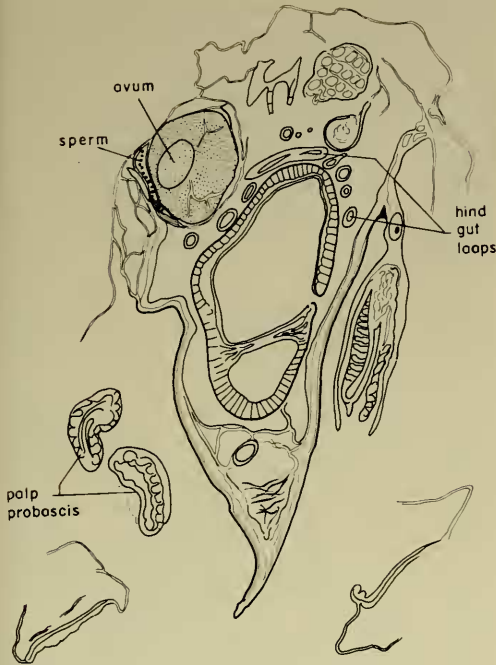
Figure 19. *Microgloma turnerae* (Sanders and Allen). Transverse section through stomach and gonad (including first ovum).
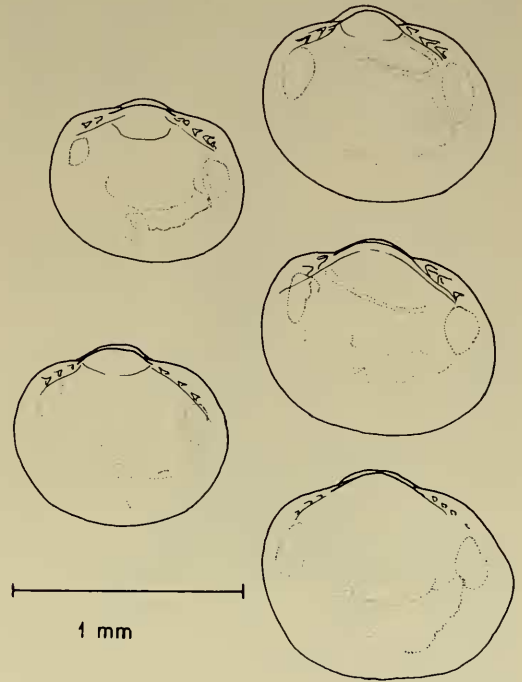

Figure 20. Lateral view of a series of specimens of *Microgloma turnerae* to show changes in shape with increasing size.

Respiratory needs perhaps diminish with increasing depth, and an increase in palp size with consequent increase in ciliation compensates for loss of ctenidial ciliation. It may also reflect a loss of sorting ability of the gills which again is compensated for by an increase in the sorting area of the palp. This latter correlation is perhaps not so significant in abyssal deposit-feeding bivalves since organic matter in sediments are refractory in the deep sea and deposit feeders must process large quantities of material. It might be noted that in the Nuculanacea, where the ctenidial axis is muscular and gills may form a pump diaphragm, progressive reduction of the ctenidium with increasing depth, while occurring, is not so great.

The small size of the Pristiglomidae in itself may be a modifying factor in their respiratory needs. Simple diffusion across a small body volume may supply much of the oxygen required and may explain in part that *P. alba* (1.90 mm maximum total length) has only two pairs of gill filaments to each ctenidium—the least recorded for any adult bivalve—while *P. nitens* (3.54 mm maximum total length) has eight to thirteen pairs. Yet, even in *Microgloma*, which must be one of the smallest if not the smallest recorded bivalve, ctenidia are not lost altogether and there are six pairs of gill filaments in both species.

In general, because the Nuculacea are not rostrate or posteriorly elongate, the palp proboscides are relatively short in comparison with those of the Nuculanacea, particularly in those species which are greatly extended posteriorly. In *Pristigloma*, and *P. alba* especially, because of the great size of the palp in relation to the shell length and the fact that the posterior limit of the palp lies close to the mantle edge, the palp
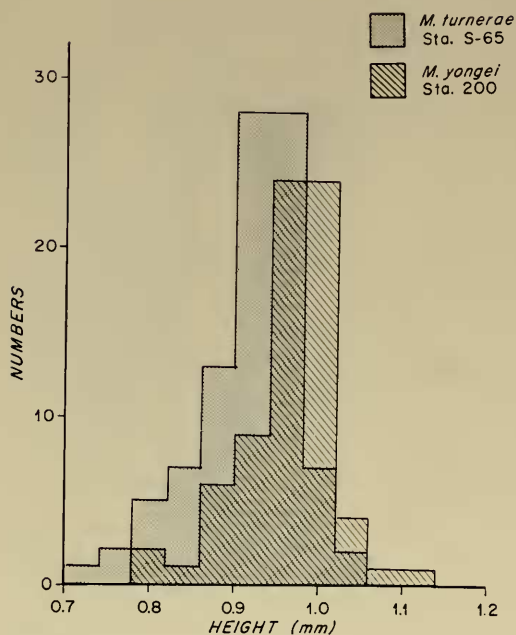
Figure 21.   Size/frequency histogram of one sample each of *Microgloma yongei* and *M. turnerae.*

proboscides are proportionately shorter. In *Microgloma* the palp does not lie as close to the mantle edge as in *Pristigloma* and the palp proboscides are relatively longer than in the latter genus.

Because food is not plentiful and much is refractile (Sanders and Hessler, 1969), and probably difficult to digest, the gut of deep-sea protobranchs, and of the Pristiglomidae in particular, is modified. Thus, while the stomach is similar in design to that of shallow-water protobranchs (Yonge, 1959; Purchon, 1956), in *Pristigloma alba* and *Microgloma* sorting ridges are only two or three in number and these are not very pronounced. However, the stomach remains relatively large, as does the style sac, and together they take up most of the available body space.

The hindgut in shallow-water species such as *Nuculana* forms a single loop on the right-hand side of the stomach. In deep-sea species the hindgut is extended and, as such, poses a problem in the disposition of an elongate tube. Many different arrangements have been evolved, as will be apparent from future publications. In *Pristigloma* the hindgut is looped to the right and left of the stomach, the loops being carried from one side to the other behind the stomach. In contrast, in *Microgloma* there are three coils around the top of the stomach in a horizontal plane and also an additional loop on each side. In all protobranchs the final straight section of
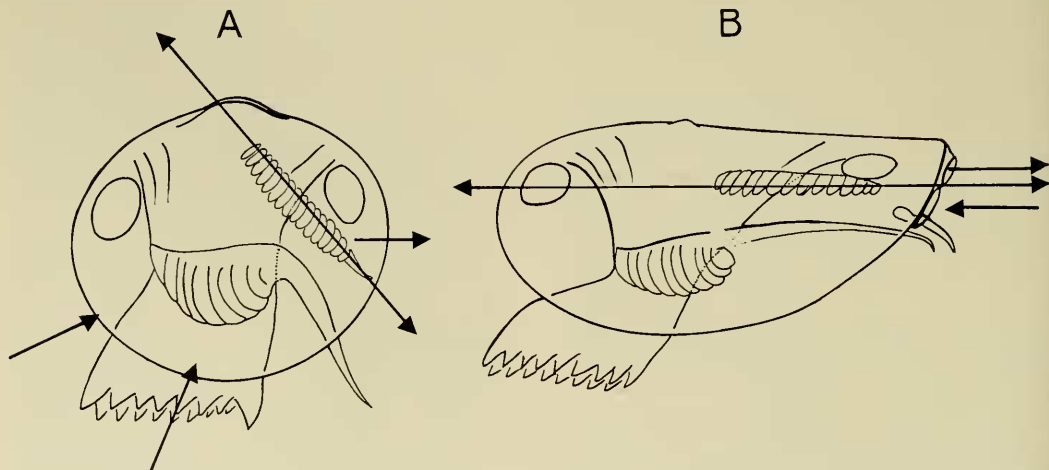

Figure 22.   Relationship between water flow and the gill axis in a) the nonsiphonate Pristiglomidae and b) a generalized siphonate nuculanacean.

gut to the anus always originates on the right side. Unlike *Abra* (Allen and Sanders, 1966) the closely packed loops never coalesce into a single sac modified for the bacterial decomposition of organic matter in fecal pellets. Digestion is extracellular in the protobranchs, and enzymes from the digestive glands (and possibly elsewhere) can function in the hindgut. A bacterial flora has not been observed in the deep-sea protobranchs. The hindgut loops are usually closely packed and adjacent lengths frequently pass material in opposite directions, thus giving rise to a contra-flow effect typical of blood systems (Scholander, 1968). We are unable to determine whether diffusion takes place across the membranes of such adjacently opposed segments.

In all protobranchs, fecal material is compacted to form rods. It will be shown later that the ctenidial axes in many protobranchs act as a guide for the disposal of feces to the outside. In the Pristiglomidae, however, the extensions of the ctenidial axes are not attached and do not appear to function in this way. Thus fecal rods are frequently seen in the ventral part of the mantle cavity (Fig. 3) of pristiglomid species, and occasional specimens have been observed with a fecal rod partially extruded and extending across the gap between the ctenidial axes into the lower half of the mantle cavity. Normally, ciliary currents across transversely arranged gill plates will give rise to a posteriorly directed water flow that will tend to carry fecal material out with the exhalent current. However, the ctenidia are so reduced in the pristiglomid species that this flow is probably too weak to function in this way. It seems possible that the enlarged heel of the foot of the Pristiglomidae is used in ejecting the rods posteriorly from the mantle cavity. The position of the rods behind and adjacent to the heel is such that the normal foot movement of the animal will eject them posteriorly.

The function of the "byssal" gland is obscure; it is universally present but varies in size within the Protobranchia. In the Pristiglomidae it is well developed with no evidence that byssus threads are produced. The detailed histology of this gland in the Protobranchia as a whole will be the subject of a later paper.

FUNCTIONAL MORPHOLOGY OF THE HARD-PART ANATOMY IN THE PRISTIGLOMIDAE

The ventral position of the adductor muscles (in relation to the height of the shell) reduces the tendency of the valves to shear. The relative size of the adductors, the robustness of the shell, the thickness of the hinge plate, the number and structure of the teeth and the size of the ligament are interrelated. The adductor muscles are proportionately larger in the heavier-shelled microglomids, which possess a relatively strong hinge plate, well-developed chevron teeth, and a large amphidetic internal ligament. In contrast, the thin-shelled pristiglomids have a weak hinge line and few teeth, some or all of which are low and lamellar in form. The differences between the two genera are particularly apparent when *Pristigloma alba* is compared with *Microgloma* (to which it is similar in size). Thus, *P. alba* has small adductor muscles, an inflated and very fragile shell, and a thin weak hinge line. The hinge area is further differentiated by the posterior plate bearing three reduced lamellar teeth and the anterior hinge plate with one or two weak ridges.

The internal ligament differs in the two genera. The large amphidetic, bean-shaped ligament of *Microgloma* correlates with the shell symmetry, the equal size of the adductor muscles, and the symmetry of the few low chevron-shaped teeth on the hinge plates. The large, somewhat ventrally sloping, opisthodetic ligament of *Pristigloma* is correlated with the asymmetry of the body (there being a larger proportion of the animal anterior to the umbo), the larger size of the anterior as compared to the posterior

adductor muscle, and the shallow, asymmetrical hinge plates. Again, these characters are more developed in *P. alba* than in *P. nitens*. The horizontal oval and elongate form of both ligaments counteracts shearing.

MINIATURIZATION

The species of *Microgloma*, although perhaps the smallest of bivalves, remain complex morphologically and structurally. Restraints towards reducing the length of the hindgut are imposed by the poor feeding conditions for these and other deposit feeders in the deep sea. The sediments are uniformly low in organic matter (Sanders, Hessler, and Hampson, 1965) and, more important, such organic matter that is present is refractory (Sanders and Hessler, 1969). Therefore, deposit-feeding bivalves process large quantities of sediment with the result that the hindgut is relatively long, and in *Microgloma,* the elongate hindgut is manifested by its complex looping and coiling about the stomach.

The microglomid response to miniaturization has not been an obvious reduction in cell number but rather a marked diminution in cell size. On a tissue-by-tissue comparison with *Nucula cortica* (a small species, 2.5 mm total length), body cells in *Microgloma turnerae* are only 8.5 percent as large by volume. A similar trend can be shown for *Pristigloma* (8.7%) (Table V).

The single major exception to this generalization is in the reproductive system. Only two mature eggs are present in the oviducts of *M. turnerae* and *M. yongei,* certainly the smallest egg number yet reported for a bivalve. However, such a pronounced reduction in egg number is attributable to the absence in the protobranchs of the planktotrophic mode of reproduction with its production of small eggs. In bivalves with lecithotrophic development, eggs are at least 90 μ in length (Ockelmann, 1965). With such an astonishingly low reproductive potential, mortality must be drastically

TABLE V.   MEAN CELL MEASUREMENTS OF VARIOUS TISSUES (AVERAGED DIMENSIONS (μ) OF TEN CELLS) OF THREE SPECIES OF DEEP-SEA PROTOBRANCHIA

	Microgloma turnerae	*Nucula granulosa*	*Pristogloma nitens*
Style sac			
Height	9.6	21.2	17.2
Width	7.8	11.2	5.4
Hindgut			
Height	5.2	25.9	6.1
Width	4.9	16.8	4.4
Palp epithelium			
Height	8.4	15.9	7.4
Width	4.1	9.0	5.1
Foot epithelium			
Height	7.8	23.7	10.4
Width	6.8	10.0	5.8

reduced to allow sufficient numbers of young to reach sexual maturity and so maintain the species. Mortality can be reduced by the suppression of a planktonic stage and the adoption of direct development; such an evolutionary strategy together with miniaturization of the genus may explain the apparently anomalous findings of a lecithotrophic egg size of 115–120 μ in *M. turnerae* and *M. yongei* coupled with a prodissoconch size of 260 μ and 290 μ respectively, indicative of *direct* development. The size of the gonadal apertures in the minute microglomids imposes a rigid upper limit on the size dimensions of an egg that can be passed. Egg sizes that are correlated with direct development, 150 μ–200 μ (Ockelmann, 1965), are too large to pass through the oviduct. We suggest that the largest egg size that can be so discharged falls within the size range given for the lecithotrophic egg although the very small clutch size dictates a direct mode of development, and this is supported by the large size of the prodissoconch. Egg production is probably continuous and the larvae may be lecithotrophic for a very short period of time. The restricted patterns of distribution in the microglomids are certainly compatible with a direct mode of development.

DISTRIBUTION PATTERNS

The two genera of the Pristiglomidae have contrasting patterns of distribution. Both *Pristigloma nitens* and *Pristigloma alba* are broadly distributed vertically at depths between 2000 m and 5000 m and they are present at many of the stations in these depths. Yet despite the fact that they are consistent elements of the fauna, these bivalves are never represented by more than a few individuals and they usually comprise less than 1 percent of the Protobranchia in the sample. They also have broad horizontal or zoogeographical distributions. We have now collected *P. alba* from the North American Basin, the Canaries Basin, the Angola Basin, the Brazil Basin, and the Argentine Basin and *P. nitens* from the same five basins as well as the West Europe Basin.

Microgloma turnerae and *Microgloma yongei*, on the other hand, appear to be narrowly distributed both horizontally and vertically. *M. turnerae* has been collected from mid-bathyal to upper abyssal rise depths at but three stations in the West Europe Basin and a single locality in the Canaries Basin. *M. yongei* is known from three upper abyssal rise–lower slope stations, one in the Cape Verde Basin, and two in the Angola Basin. Yet, when they are present, the microglomids are often numerically major constituents of the protobranch bivalves. At station S-65, *M. turnerae* comprised more than 50 percent of the sample while *M. yongei* comprised almost 15 percent of the protobranchs at station 175 and 58 and 9.5 percent at stations 200 and 201.

SUMMARY

Extensive and continuing sampling of the benthic fauna at bathyal and abyssal depths of the Atlantic has yielded very great numbers of protobranch bivalves. Examination of these collections has revealed many new species and many varied morphologies, indicating that the great radiation of this group has taken place in the deep sea. Such unique and varied material makes possible comprehensive studies of this relatively poorly known subclass. Some of the components of these investigations are the comparative anatomy of both soft and hard parts, functional morphology *per se* and in relation to abyssal life, changes in form with growth, mode of reproduction, and ecology.

To put subsequent studies in perspective an advance outline classification of the major taxa is given. This is followed by the analysis of a new family of the Nuculacea, the Pristiglomidae, which comprises the genera *Pristigloma* (previously placed in the family Nuculanidae, here raised to superfamily status), and *Microgloma*, a new genus.

Two species of *Pristigloma* are found in the samples, *P. nitens* and the new species *P. alba*. Both are broadly distributed, vertically and horizontally, in the deep Atlantic, being most frequently found between 2500 m and 5200 m. Despite their wide range and frequent presence, they usually constitute less than 1 percent of the total protobranch fauna at any one station. They are characterized by extremely reduced gills (two pairs of gill plates only in *P. alba*), exceptionally large palps, and an elongate hindgut that makes at least four separate loops to either side of the body.

The genus *Microgloma* is also represented by two species, both new, *M. turnerae* and *M. yongei*. These are closely related and, in contrast to *Pristigloma*, have a much more circumscribed distribution in depth and geography. *M. turnerae* is restricted to the West Europe and Canaries basins at 1000–2300 m and *M. yongei* is found only in the Cape Verde and Angola basins at 2000–2700 m. Unlike *Pristigloma*, *Microgloma* is present at relatively few stations but may make up a significant fraction of the total protobranch population. They are among the smallest bivalves known and miniaturization has been accomplished largely by reduction in cell size. However, in the case of the gonads there is a

drastic reduction in germ-cell numbers, with only two ova maturing at any one time.

REFERENCES

ALLEN, J. A. 1958. The basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). Phil. Trans. r. Soc. London, **24:** 421–484.

———. 1968. The functional morphology of *Crassinella mactracea* (Linsley) (Bivalvia: Astartacea). Proc. malac. Soc. London, **38:** 27–40.

———. 1971. Evolution and functional morphology of the deep water protobranch bivalves of the Atlantic. Proc. Joint Oceanogr. Assembly, Tokyo, 1970: 251–253.

——— AND SANDERS, H. L. 1966. Adaptations to abyssal life as shown by the bivalve *Abra profundorum* (Smith). Deep-sea Res., **13:** 1175–1184.

——— AND ———. 1969. *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont. Malacologia, **7:** 381–396.

ATKINS, D. 1936. On the ciliary mechanisms and interrelationships of lamellibranchs. Pt. I. Some new observations on sorting mechanisms in certain Lamellibranchs. Quart. J. microsc. Sci., **79:** 181–308.

CLARK, A. H., JR. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. Bull. natn. Mus. Canada, **181:** 1–114.

COX, L. R. 1959. The geological history of the Protobranchia and the dual origin of taxodont Lamellibranchia. Proc. malac. Soc. London, **33:** 200–209.

———. 1960. Thoughts on the classification of the Bivalvia. Proc. malac. Soc. London, **34:** 60–88.

DALL, W. H. 1889. A preliminary catalogue of the shell-bearing marine molluscs and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. Bull. U.S. natn. Mus., **37:** 1–221.

———. 1895. Contributions to the Tertiary fauna of Florida, with special reference to the Miocene silex beds of Tampa and the Pliocene beds of the Caloosahatchie River. Tertiary mollusks of Florida Pt. III. A new classification of the Pelecypoda. Trans. Wagner Free Inst. Sci., **3:** 485–570.

———. 1900. Some names which must be discarded. Nautilus, **14:** 44–45.

HESSLER, R. R. AND SANDERS, H. L. 1967. Faunal diversity in the deep sea. Deep-sea Res., **14:** 65–78.

JEFFREYS, J. G. 1876. New and peculiar mollusca of the *Kellia, Lucina, Cyprina* and *Corbula* families procured in the 'Valorous' Expedition. Ann. Mag. nat. Hist., ser. 4, **18:** 424–436.

———. 1879. On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions, 1869–1870. Pt. II. Proc. zool. Soc. London, 553–588.

McALESTER, A. L. 1964. Preliminary suggestions for a classification of nuculoid bivalves. J. Paleont., **38:** 397–400.

OCKELMANN, K. W. 1965. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. Malacologia, **5:** 25–35.

PURCHON, R. D. 1956. The stomach in the Protobranchia and Septibranchia (Lamellibranchia). Proc. zool. Soc. London, 511–525.

———. 1958. Phylogeny in the Lamellibranchia. Proc. Cent. Bicent. Congr. Biol. Singapore, 1958: 69–82.

———. 1959. Phylogenetic classification of the Lamellibranchia with special reference to the Protobranchia. Proc. malac. Soc. London, **33:** 224–230.

SANDERS, H. L. AND HESSLER, R. R. 1969. Ecology of deep sea benthos. Science, **163:** 1419–1424.

———, ———, AND HAMPSON, G. R. 1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. Deep-sea Res., **12:** 845–867.

SCHOLANDER, P. F. 1958. Counter-current exchanges—a principle in biology. Hvalradets Skrifter, No. 44: 1–24.

SMITH, E. A. 1885. Report on the Lamellibranchiata collected by H. M. S. Challenger during the years 1873–1876. Rept. Sci. Res. Challenger, Zoology, **13:** 1–341.

STASEK, C. R. 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia, Nuculidae) with an evaluation of the role of the protobranch organs of feeding in the evolution of the Bivalvia. Proc. zool. Soc. London, **137:** 511–538.

THIELE, J. 1934–1935. Handbuch der Systematischen Weichtierkunde. Dritter Teil, Classis Bivalvia. Jena. Pp. 779–1154.

VERRILL, A. E. 1884. Second catalogue of Mollusca recently added to the fauna of the New England Coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. Trans. Connecticut Acad. Arts Sci., **6:** 139–294.

———. 1885a. Third catalogue of Mollusca recently added to the fauna of the New England Coast and the adjacent parts of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. Trans. Connecticut Acad. Arts Sci., **6:** 395–452.

————. 1885b. Results of the Explorations Made by the Steamer ALBATROSS off the Northern Coast of the United States in 1883. Ext. from Ann. Rept. Comm. Fish and Fisheries, 1883. Washington: Government Printing Office. Pp. 503–699.

———— and Bush, K. J. 1897. Revision of the genera of Ledidae and Nuculidae of the Atlantic Coast of the United States. Amer. J. Sci., 3: 51–63.

———— and ————. 1898. Revision of the deep-water mollusca of the Atlantic Coast of North America with descriptions of new genera and species. Pt. I. Bivalvia. Proc. U.S. natn. Mus., 20(1139): 775–901.

Yonge, C. M. 1939. The protobranchiate Mollusca; a functional interpretation of their structure and evolution. Phil. Trans., B, 230: 79–147.

————. 1959. The status of the Protobranchia in the bivalve mollusca. Proc. malac. Soc. London, 33: 210–214.